

NUTRITIONAL VALUE OF THE AMMONIUM ION FOR
HIGHER GREEN PLANTS, ESPECIALLY
AGRICULTURAL FORMS

BY
JOSÉ H. PARDO

A DISSERTATION

SUBMITTED TO THE BOARD OF UNIVERSITY STUDIES OF THE JOHNS
HOPKINS UNIVERSITY IN CONFORMITY WITH THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

BALTIMORE, MARYLAND
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AMMONIUM IN THE NUTRITION OF HIGHER GREEN PLANTS

By JOSE H. PARDO

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I. INTRODUCTION

POSSIBLE sources of nitrogen for the metabolism of higher plants are nitrates, nitrites, ammonium compounds and a great variety of organic nitrogen compounds, such as amino acids and amides. Some of these are commonly taken up from the soil solution, like water and the salts that do not supply nitrogen, while some are usually not absorbed as such but are formed within the plant from simpler compounds previously absorbed. It has been suggested (85) that some seed plants, such as wheat, may actually assimilate small amounts of molecular nitrogen but most physiologists and agricultural chemists consider nitrification as probably confined to lower forms such as the nitrifying bacteria of the soil and the nodule-forming symbionts.

Although there is some evidence (99, 115, 154) that nitrites may be absorbed and assimilated by higher plants, yet it has not been shown that these compounds are commonly utilized directly, indeed they are usually omitted when nitrogen sources for higher plants are considered.

While there is no doubt that some ammonia (NH_3) may enter the plant through leaves or roots, from the surrounding air or from the soil, yet only a very small portion of the nitrogen required can generally be thus absorbed, and it is difficult to consider NH_3 as actually entering living cells, for it appears to react with water to give the NH_4 ion. Harvey states (54, p. 68), however, that this gas, applied through the leaves, is "much more toxic than it should be from the alkaline reaction it produces in the cell," resulting in "the overgrowth of tissues into hyperplasias if the concentration is very low." This observation raises questions that are clearly worthy of special study. Specific effects produced by foliar absorption of NH_3 may be related to some ions other than NH_4^+ itself, or to some other special conditions accompanying the presence of NH_4^+ when due to leaf absorption of NH_3 rather than to root absorption of ammonium salts.

Root absorption of amino acids and other organic nitrogen compounds has been reported (81) by some experimenters, and such compounds are probably ab-

sorbed through leaves, haustoria, etc., in some special forms like insectivorous plants and parasites, but these compounds do not generally appear to be a significant external source of metabolic nitrogen for higher green plants. Salts of ammonium with organic acids should also be mentioned as possibly absorbed from the soil in some instances, but they seem to be of minor general importance.

It seems to be well established, however, that nitrate nitrogen is generally acceptable to all higher plants and that ammoniacal nitrogen is also acceptable under suitable conditions, at least, to many forms. Both of these sources of nitrogen are commonly present in the soil solution and in the waters of lakes and streams, but naturally their concentrations are usually relatively low. Nitrates are readily leached from soils and they are apt to be reduced to nitrites or even to ammonium salts through the action of microorganisms when conditions are suitable. On the other hand, ammonium salts, although they appear to be held in the soil to a greater extent than nitrates (68), are subject to alteration by soil bacteria, being thus oxidized to produce nitrites or nitrates. Soil bacteria may also transform a nitrite into a nitrate or into an ammonium salt, such as $(\text{NH}_4)_2\text{CO}_3$. Furthermore, the possibility that roots may sometimes exert an oxidizing or a reducing influence upon nitrogenous substances in the surrounding solution has not been excluded. It is therefore difficult to show clearly by simple experiments just what nitrogen compounds are actually absorbed by plant roots, even when it is possible to exclude nitrifying and denitrifying bacteria from some of the experimental cultures, and it is not easy to be sure that these bacteria have been excluded.

Nevertheless, experimental comparisons

may be easily made with reference to the effects produced on growth and development by different nitrogen compounds when added to soils or sand cultures or when incorporated into culture solutions, and a great deal of experimentation has been devoted to such comparisons. From this kind of experimentation, taking account of the common possibilities of nitrification and denitrification, present agricultural theory with regard to nitrogen fertilizers has been developed.

Boussingault (18) seems to have been the first to show that nitrates are a very satisfactory source of metabolic nitrogen for many green flowering plants. He discovered the occurrence of nitrification in the soil, by which process ammonium salts and nitrites become oxidized to form nitrates; numerous investigators have subsequently studied nitrification in culture media. As soon as this process became appreciated most physiologists and soil chemists argued that the absorption and assimilation of ammonium salts was at least problematic, since these might be converted into nitrates, which, in turn, would be absorbed and assimilated.

Schattenmann's (138) field experiments with sulphate, chloride and phosphate of ammonium, which were referred to by Dumas (29), are interesting historically, as at least among the very earliest published evidences of the important rôle played by ammonia in bringing about the beneficial fertilizer effects obtained from the field use of stable manure. Of course these did not touch on the question whether ammonium salts are directly assimilated or are first converted into some other nitrogen compound, but they showed that the application of these salts to the soil led to markedly improved growth and larger crops in many instances. Schattenmann noted that alfalfa and clover failed to respond to this fertilizer treat-

ment. Dumas stated that Schattenmann had discovered this "rôle de l'ammoniaque dans la végétation" before 1835, whereas Liebig's statement (84) on that topic appeared only in 1840, in which year Dumas himself had expressed the same ideas, derived in part from a personal letter received by him from Schattenmann in 1836.

By the end of the nineteenth century students of plant nutrition generally agreed that ordinary green plants (with roots in soil or solution and stems and leaves in air) derive practically all of their assimilated nitrogen from the soil, either from salts of nitric acid (the NO_3 ion) or from ammonium compounds (the NH_4 ion). In Ewart's English translation of Pfeffer's *Plant Physiology*, which appeared about the beginning of the present century and which may be taken as fairly representative of the status of plant physiological knowledge at that time, it is stated (116, vol. I, p. 392) that green plants growing on well aerated soils (i.e., soils with considerable water content, but not nearly saturated with water) usually prefer their nitrogen in the form of nitrates. Other more specific statements from the same publication are as follows:

"Most Phanaerogamic plants grow best when supplied with nitrates, but ammonium salts are more suitable for others. . . ." (*ibid.*, p. 403). "In Phanaerogams ammonium salts are always assimilated when present, however abundant nitrates may be" (*ibid.*, p. 404). "Neither Phanaerogams nor Algae appear to have the power of forming nitrates from ammonium salts by oxidation. . . ." (*ibid.*, p. 405).

Preference of swamp rice, notably when young, for ammonium salts rather than nitrates is especially mentioned (*ibid.*, p. 404) and it is added that "this is probably often the case in plants which grow in swampy or badly aerated soil, where the process of nitrification takes place slowly

or not at all." It is pointed out, further, that "under natural conditions Phanaerogams rarely absorb organic nitrogen compounds . . ." although such substances as urea, glycolic acid, asparagin, leucin, tyrosin, hippuric acid, etc., may be absorbed and utilized as sources of nitrogen by flowering plants as well as algae under some conditions.

II. RECENT TEXT-BOOKS, HANDBOOKS AND GENERAL DISCUSSIONS

Authors of text-books and handbooks that have appeared in the last three decades appear to be in general agreement on the point that nitrates are generally utilized by ordinary green plants, but the question whether ammoniacal nitrogen may be commonly or only occasionally utilized by such forms seems to have remained generally about as Pfeffer left it. This question is specially difficult on account of the possibility that an ammonium salt, in an experimental soil solution or in a liquid medium as well as in ordinary field soils, may undergo oxidation with the result that the ammonium ion may seem to be absorbed and assimilated by the plants of an experiment even if nitrogen assimilation may actually be wholly or partially dependent on the absorption of the nitrate ion. The difficulty is further augmented by the logical possibility that—in some kinds of experiments at least—the ammonium ion may perhaps be absorbed to a considerable extent without being actually assimilated.

Most text-book writers agree that, while nitrates are generally more suitable for the nitrogen nutrition of higher plants, yet ammonium salts, other than the nitrate, are also assimilable, at least by many forms. One gets this idea from the books of Barton-Wright (10), Benecke and Jost (12), Green (43), Harvey (54), James (65), Jost (66), Nathansohn (104), Peirce

(112), Russell (135), Thatcher (149) and Torrey (152). In the American edition of Palladin's *Plant Physiology* (107) it is stated that "nitrates act chiefly, if not exclusively, as the source of nitrogen for higher plants," but at the same time references are given to some experiments that seem to indicate the direct utilization of ammoniacal nitrogen by some of these plants. Other writers consider that nitrates and ammonium salts are about equally suitable for the nutrition of higher plants in general; for example, Euler (36), Kostychev (76), and Maximov (91). The last-named author says (91, p. 54) that "they cannot be considered a more inferior source of nitrogen for plants than the nitrates."

Some writers of text books appear to doubt the general assimilability of ammoniacal nitrogen by higher plants. Raber (133, p. 77) says that ammonium salts are "of doubtful value in the direct nutrition of plants." Nathansohn (104), Peirce (112) and Leclerc du Sablon (136) appear to regard the question of ammonium assimilation as of minor importance, since ammonium salts are apt to be oxidized to nitrates in the soil. From the purely practical or technological viewpoint this may be a satisfactory view (since any soil may be supposed to contain nitrifying organisms as long as their absence has not been actually shown, which might in many cases be difficult in the field), but there seems to be no reason to doubt that the ammonium ion from ammonium salts may sometimes be a very important source of nitrogen, especially when the supply of nitrates is too limited. Hall appears to be inconsistent when he writes, in two books published in the same year, that "the higher plants doubtless take in the nitrogen they require as ammonia" (46, p. 221), and that "if ammonium salts are to feed the plants, they must be nitrified" (47, p. 67).

Still other authors of books on plant physiology seem to avoid the question of the direct assimilation of the ammonium ion by limiting their statements to the question of its absorption. In this group are Clements (21), Detmer (27), Duggar (30), Honcamp (58), Lepeschkin (83), Lyon, Fippin and Buckman (89), and MacDougal (90). Still others, such as Atkins (7), Barnes (22), Darwin and Acton (25), Ganong (39), Kolkwitz (73) and Timiriazeff (151), appear to leave the question of ammoniacal absorption and assimilation out of account altogether.

That plant forms seem to differ with respect to their ability to absorb or to absorb and assimilate ammonium salts and with respect to their "preference" for ammoniacal or nitrate nitrogen, was clearly stated by Pfeffer, as mentioned above, and similar statements are found in the more recent books of Linsbauer and Linsbauer (86), Lyon, Fippin and Buckman (89), Haas and Hill (45), and Jost (66). On this topic Miller's very recent book states (100, p. 503) that "the evidence indicates that some plants grow equally well with both nitrates and ammonium salts and that others, although assimilating ammonium nitrogen in the absence of nitrates, seem to prefer nitrates." Some of these differences may perhaps be related to the so-called "physiological acidity" of some ammonium salts when added to soil in which plants are grown. Thus Kostychev (76, p. 116) observes that "ammonia is nearly as good a source of nitrogen for seed-plants as nitrates whenever the plants can tolerate the resultant acid soil reaction or when the soil constituents at once neutralize the acids that are formed." On the other hand, there seems to be no reason to suspect that absorption of nitrate nitrogen may ever produce harmful effects through lowering of the H-ion concentration of the medium. It is commonly supposed that

plants differ with respect to their tolerance towards soil acidity and that such differences may explain some of their differences with respect to apparent nitrogen preferences. Several writers mention that plants seem to tolerate higher concentrations of the NO_3 ion than of the NH_4 ion. This point is clearly indicated by Euler (36), Jost (66) and Maximov (91).

Czapek (23, p. 307 *et seq.*) gives an account of the status of this problem of nitrogen nutrition about 1924, with a number of references to original contributions.

A valuable brief general discussion of the problem of the assimilation of the NH_4 ion by ordinary plants is to be found in Hutchinson and Miller's paper (63), which is accompanied by a bibliography of contributions that appeared before 1909. In their conclusion we read: "Some plants grow equally well with ammonium salt or nitrate as source of nitrogen. Other plants, while assimilating ammoniacal nitrogen in the absence of nitrates, appear to prefer nitrates. It is less certain whether ammonium salts can ever produce better final results than nitrates although we have indications that this may be the case." A brief discussion concerning what kinds of nitrogen compounds may supply nitrogen to plants was recently presented by Allison (2), who wrote:

"No doubt nitrate nitrogen is the best source of nitrogen for the majority of plants and, under conditions where nitrates are present in relatively high percentages or where the conditions for rapid nitrification are favorable, it is safe to say that most of the nitrogen assimilated is in this form." "Nitrites may also be utilized by higher plants where the concentrations are low but they are so rapidly oxidized to nitrates that they ordinarily occur only in traces in soils and there is little reason for believing that plants secure much of their nitrogen in this form." "The writer has merely taken for granted that under average field conditions nitrate nitrogen is probably the most important nitrogen source for crops, but has pointed out that other forms may also be utilized to a greater extent than has generally been supposed."

Another representative general statement about the relative nutritional values of NH_4 and NO_3 may be found in Hoagland's recent paper (55, p. 628). He says that the H-ion concentration of the medium is very important when NH_4 is the source of nitrogen," the rate of absorption of nitrogen increasing with increase of p_{H} ." He also points out that ammonium salts are more apt to be injurious to plants than are nitrates, unless various non-nitrogen culture conditions—including temperature and illumination as well as H-ion concentration—are carefully adjusted. Although NH_4 may be quite suitable as nitrogen source under properly adjusted conditions, yet "there is, in general, a greater range of safety in the use of nitrate nitrogen for the majority of agricultural plants studied."

Pirschle (119) wrote that both NO_3 and NH_4 are generally assimilated by higher plants, but that NO_3 may be superior to NH_4 , especially when the medium is poorly buffered. In the same paper Pirschle presents an interesting brief review of the manner in which theory has altered in the last three decades. That review may be summarized as follows. In the last century it was at first held, following Kühlmann and Liebig, that NH_4 was the only nitrogen source for higher plants. When NO_3 was supplied it was supposed to be reduced to NH_4 in the soil, before being absorbed by roots. Boussingault's practical experiments (18) led to the opposite idea and then NO_3 was considered as the only—or at least the best—nitrogen source for higher plants. Through the work of many investigators it is now generally thought that both NH_4 and NO_3 may be assimilated by higher plants, but it is pointed out that they do not operate alike.

Ammonium salts are said to be "physiologically acid," while nitrates are physiologically neutral or alkaline. This

distinction was first explained, following Ad. Mayer (93), by supposing that NH_4 is absorbed more rapidly than SO_4 (when $(\text{NH}_4)_2\text{SO}_4$ is supplied, for instance), thus increasing the concentration of SO_4 and of the hydrogen ion in the medium. The increasing acidity was regarded as acting toxically on many plant forms and consequently NH_4 appears to be a very poor source of nitrogen for such forms. On the other hand, when NaNO_3 is supplied it was supposed that NO_3 is absorbed more rapidly than Na, with consequent *decrease* in the hydrogen-ion concentration of the medium, but that decrease may be hindered or prevented by extrusion of anions from the roots. Prianischnikow (128) and others went on to show, however, that $(\text{NH}_4)_2\text{SO}_4$ may be as good as NaNO_3 , or even better, if acidification by the use of the former is prevented. Thus theory tended to revert to the older view of Liebig, but with the important difference that Liebig thought of reduction of NO_3 to NH_4 as occurring in the medium before absorption, while Prianischnikow thought that the NO_3 absorbed is reduced to NH_4 within the plant, as the first step leading toward the formation of amino-acids. There is much reason for supposing that NH_4 is actually the main internal source of nitrogen in amino-acid formation and if that is true it seems to follow that an ammonium salt should be superior to nitrates as external source of nitrogen, for plants that cannot tolerate high hydrogen-ion concentration in the medium, if and when the effect of physiological acidity is counteracted.

Recent studies on agricultural soils have led to further development of the theory of the physiological acidity of ammonium salts. A review of this advance was presented by Pierre (118) and a brief summary thereof may be found in Russell's textbook (135, p. 228). Many students of

this question regard it as probable that nitrification in the soil, rather than selective absorption by roots, is the cause of the soil acidification that results from the use of $(\text{NH}_4)_2\text{SO}_4$ as fertilizer. According to this view, the NH_4 is first absorbed by the soil, uniting with soil anions and releasing some of the exchangeable soil bases to form sulphates with the released SO_4 . Then the resulting absorbed ammonium salts of the soil are oxidized by nitrifying organisms, to produce nitric and soil acids, which are in turn neutralized by further reaction with remaining soil bases. Thus NH_4 is first oxidized to NO_3 , which is the actual nitrogen source that is absorbed by the plants, and the increasing acidity of the soil is due to soil acids that are set free by the process of nitrification. It needs to be pointed out that this theory has been developed for soil cultures, in which exchangeable soil bases and acids are available, and that it supposes the rate of nitrification of ammonium salts in a soil to be greater than the rate at which NH_4 may be absorbed directly by the plants growing in that soil. In solution cultures in which $(\text{NH}_4)_2\text{SO}_4$ is the source of nitrogen increased acidity of the medium may be due apparently to either nitrification or to differential absorption. The equation for nitrification may be: $(\text{NH}_4)_2\text{SO}_4 + \text{O}_2 \rightarrow (\text{nitrification}) \rightarrow 2\text{HNO}_3 + \text{H}_2\text{SO}_4 + 2\text{H}_2\text{O}$. The medium would thus become more acid without reference to absorption by the plants. On the theory of differential absorption NH_4 would be absorbed by the roots, leaving an excess of SO_4 to produce increased acidity in the medium.

The theory concerning utilization of NH_4 and NO_3 by higher green plants has been still further complicated on account of the findings of recent experimenters who have dealt with the influence of the

hydrogen-ion concentration of the medium on the suitability of these nitrogen sources for higher plants. Pirschle has dealt with this phase of the problem in several contributions and Mevius (97) has given it special attention. The last-named author has published extensive bibliographies (97, 98). Some of these H-ion relations will receive mention in the following section of the present paper. All that can be said about them in a brief general summary is that modern experimentation on the relative suitability of NH_4 and NO_3 as nitrogen sources involves careful attention to the H-ion concentration of the medium. General agreement as to these relations has not yet been obtained; different kinds of plants appear to behave differently and many other non-nitrogen conditions are apparently important in determining whether NH_4 may equal or may even exceed NO_3 in suitability.

It is not the writer's purpose to attempt here a critical review of the theoretical aspect of this problem; no clear picture of its present status is possible without an appreciation of the numerous experimental results that have been reported. Since these are not generally satisfactorily comparable (doubtless largely because of the employment of many different plant forms and many experimental techniques), the writer was led to the preparation of a sort of annotated bibliography of them and a portion of that bibliography is presented below.

III. REPORTS ON EXPERIMENTS

The numerous research articles bearing on the question of NH_4 *versus* NO_3 in the nitrogen nutrition of higher green plants are widely scattered. The present article represents a portion of the results of an attempt to summarize this part of the physiological literature. Attention is

here confined to evidence based on growth, development, configuration, general appearance and yield. The writer hopes to present subsequently a review of the literature on studies carried out from the standpoint of physiological chemistry, employing quantitative analyses of the plant material and referring to rates of absorption and to the process of assimilation itself. In many cases both of these points of view are considered in the same published contribution, but it seems advantageous to treat them separately.

Only solution-culture experiments (including sand cultures to which solutions are added) are generally considered in this review. Practical field tests of nitrogenous fertilizers, which have been carried out in great number by many workers, are not generally referred to, since such experiments inevitably involve a much larger group of unknown influences or conditions than need to be considered when physiological cultures are employed, with which much more satisfactory controls are possible. Soil cultures and field tests pertain to agriculture or ecology rather than to physiology. It needs repeated emphasis that the solutions of practical problems in agronomy and horticulture are to be sought through actual field tests, while the related scientific or theoretical problems of physiology may be approached directly only through experimental use of well-controlled solution cultures. What may be the best nitrogen fertilizers in field practice or in soil cultures, with various soils and climatic complexes and with various methods of cultivation and rotation, is a technological question, for the answering of which fundamental physiological theory is not so important as actual field experience.

In this review nitrates are generally taken as basis for comparison, in attempt-

ing to estimate, as well as possible, the efficiency of ammonium compounds. There appears to be no record of any unequivocal tests in which NO_3 was found to be very unsuitable for the nitrogen nutrition of any higher plant, although NO_3 has been equalled or surpassed in effectiveness by NH_4 . Our problem, for each plant form, is whether NH_4 has been found to be inferior, equal or superior to NO_3 . When the numerical data for comparable tests differ by not more than 10 per cent the results are considered as about equal.

Attention should be called to the fact that the term *ammonium salts* usually excludes the nitrate and *nitrates* excludes NH_4NO_3 . The last-named salt is of course both an ammonium salt and a nitrate. It is in a class by itself and requires special attention as such.

The contributions cited are presented in an arrangement of subsections according to the kinds of plants considered, the primary grouping being by plant families, which are arranged in alphabetical order. For each plant form the contributions are generally mentioned in chronological order. Numerical indices in parenthesis refer to the appended bibliography.

The material here presented was assembled in connection with a series of solution-culture experiments carried out by the writer on NH_4 assimilation by sugar cane, and some of the indications of those experiments are included here in the proper place. In the preparation of the manuscript of this review the writer has had the benefit of much helpful advice and criticism from Professor Burton E. Livingston, of the Laboratory of Plant Physiology of the Johns Hopkins University, where much of this work was done.

BALSAMINACEAE

An early experiment by Pirschle (119), with sand cultures, showed that garden

balsam (*Impatiens balsamina*) grew better when N was supplied as $\text{Ca}(\text{NO}_3)_2$ or KNO_3 than when $(\text{NH}_4)_2\text{SO}_4$ or NH_4Cl was the only nitrogen source.

BROMELIACEAE

Stewart, Thomas and Horner (147) made an extensive study of the nitrogen nutrition of pineapple (*Ananas sativa*) in Hawaii and concluded that "under field conditions the pineapple plant probably uses nitrogen in both the nitrate and ammonium forms." Their experiments showed better growth with NO_3 than with NH_4 when the N content of the nutrient solution was 160 mg. per liter, but yields from NO_3 and from NH_4 were about alike when the N content of the solution was only 40 mg. per liter. They noted that the "crown" (the top cut off from the familiar pineapple fruit) was preferable to "slips" or "suckers" in culture experiments.

CHENOPODIACEAE

Pitsch (123), using potted plants of sugar beet (*Beta vulgaris*) in sterilized soil, found that NO_3 was preferable to NH_4 with regard to root production but NH_4 sometimes gave higher sugar contents. Dikussar's experiments with sugar beet (28) gave highest weight yields with NO_3 when the nutrient medium had a p_{H} value of 5.5, but NH_4 gave better growth than was given by NO_3 when the medium was neutral.

Krüger's experiments (79) with mangel were inconclusive as to this plant's response to NO_3 and NH_4 ; in one test NH_4 gave greater root yield than was given by NO_3 but two other tests showed NO_3 to be superior. Krüger employed both sterilized and unsterilized media.

Strawberry Blite (*Chenopodium capitatum*) was found by Pirschle (121) to grow better with N supplied as NO_3 than when the nitrogen source was NH_4 , for

several different H-ion concentrations of the medium.

COMMELINACEAE

Wandering Jew (*Tradescantia fluminensis*) was included in the experimentation of Mevius (97), whose data indicate that NO_3 was superior to NH_4 in the nitrogen nutrition of this plant. But $(\text{NH}_4)_2\text{SO}_4$ gave fair growth in some experiments. Pirschle (119, 120, 121) also found, for a series of different p_{H} values of the nutrient solution and with continuously flowing as well as with unrenewed solutions, that NO_3 gave better growth of *Tradescantia viridis* and *Zebrina pendula* than was given by NH_4 . Later continuous-flow experiments by the same writer (122) showed that NH_4 was superior to NO_3 for *T. viridis*; the optimal yield was obtained with NH_4 and a p_{H} value of 7.0.

COMPOSITAE

Perotti (114) included sunflower (*Helianthus annuus*) in the experimental series by which he came to the somewhat broad conclusion that flowering plants were able to derive their needed nitrogen directly from $\text{Ca}(\text{CN})_2$. In Pirschle's tests (120, 121) sunflower gave larger yields with NO_3 as nitrogen source than when N was supplied as NH_4 , but NH_4 appeared to be superior to NO_3 when the medium had a p_{H} value of 6.0.

CRUCIFERAE

In one of Krüger's tests (79) mustard (*Sinapis*) grew as well with NH_4 as with NO_3 , but another test showed NO_3 to be superior. In Pantanelli and Severini's experiments (108, 109) mustard grew better with N supplied as ammonium tartrate or NH_4NO_3 than when it was supplied as NaNO_3 , but the latter was superior to NH_4Cl or $(\text{NH}_4)_2\text{SO}_4$. Pirschle (119, 121) found, with both continuously flowing

and unrenewed solutions, that NO_3 was superior to NH_4 for mustard, with a range of p_{H} values from 3.0 to 9.0. Another experiment (122) showed these two sources of N to be of about the same effectiveness.

Pirschle's experiments (119, 120, 121) gave results with rape (*Brassica rapa*) similar to those first obtained by him with mustard. In another experiment, with continuously flowing solutions, the greatest yields were about alike for NO_3 and NH_4 , but NH_4 was superior when the p_{H} value of the solution was 5.0. The two nitrogen sources were about alike for a p_{H} value of 6.0 and NO_3 was superior for p_{H} values of 4.0, 7.0, 8.0 and 9.0. When both NO_3 and NH_4 were supplied together (as NH_4NO_3) the optimal yields (with p_{H} value of 5.0, 6.0 or 7.0) surpassed the best yields obtained with NO_3 as the only source of N. This combination gave results like those obtained with NO_3 , when the solution had a p_{H} value of 4.0 or 8.0, and it was inferior to NO_3 with a p_{H} value of 9.0. Pirschle obtained very good growth of rape in flowing solution cultures with urea as the only source of N.

CUCURBITACEAE

Perotti's (114) results with pumpkin (*Cucurbita pepo*) were better with NO_3 than with NH_4 , and the same is true of Pirschle's (119, 120, 121) tests of this plant, for a wide range of H-ion concentrations of the medium. On the other hand, Tiedjens and Robbins (150) grew cucumber to excellent fruiting in sand cultures in which N was supplied only as $(\text{NH}_4)_2\text{SO}_4$, in a solution having a p_{H} value of 7.5. Number and quality of fruits, as well as general growth, were as good as in commercial greenhouse culture. The photograph shown by these authors (their figure 8) is remarkably striking. When the p_{H} value of the $(\text{NH}_4)_2\text{SO}_4$

solution used was 5.4 growth was slow and leaves were small and light green, but when the p_H value was afterwards changed to 7.5 the foliage became dark green and subsequent growth was rapid.

ERICACEAE

Addoms and Mounce (1) found that cranberry plants (*Vaccinium macrocarpon*) produced noticeably greater runner growth with $(NH_4)_2SO_4$ than with $Ca(NO_3)_2$.

EUPHORBIACEAE

Pirschle's (119, 121) experiments with castor bean (*Ricinus communis*), in continuous-flow as well as in unrenewed solution cultures, gave greater yields with NO_3 than with NH_4 , for a wide range of p_H values, but with a p_H value of 5.0 NH_4 was superior to NO_3 .

GRAMINEAE

Because of their great economic importance, several of the Gramineae have been extensively experimented upon and a large number of contributions by many writers are to receive brief attention in this section. The annotations are brought together in subsections, as follows: Barley, English rye grass, Maize, Millet, Oats, Rice, Rye, Sorghum, Sugar Cane, Wheat; and a final subsection presents an attempt to summarize the experimental results for this family.

Barley (Hordeum vulgare)

The literature on the nitrogen nutrition of barley appears to begin with a paper by Ville (159), published in 1875, in which he reported that this plant gave good growth when N was supplied as NH_4Cl , as well as when the source of N was an organic compound such as urea. Ville did not report on nitrates. Pitsch's extensive experiments (123) with several varieties of barley grown in pots of steril-

ized soil gave better growth with N supplied as $NaNO_3$ than when $(NH_4)_2SO_4$ was the source of N. Kossowitsch (74) grew this plant in sterilized sand and reached the conclusion that both NO_3 and NH_4 were assimilated when they were supplied together. Krüger (79) tested barley in pots with a mixture of soil and sand, sterilized as well as unsterilized, and obtained larger yields with NO_3 than with NH_4 in some experiments while other experiments showed these two sources of N to be about equally effective. Ehrenberg's experiments on barley (31) gave superior yields with NO_3 and he concluded, from an extensive study of the whole problem of nitrogen nutrition, that NO_3 was the only suitable source of N for higher plants in aerated soils, although NH_4 might be assimilated from wet, acid soils. The results of Aso and Bahadur (6) indicated that NO_3 and NH_4 were about equally suitable as sources of N for barley, and a similar conclusion may represent the results of sand-culture experiments by Pfeiffer, Hepner and Frank (117). The last-named writers reported even better yields from NH_4NO_3 than from either NO_3 or NH_4 alone. From Prianschnikow's results with sand cultures (125, 126) it appears that $(NH_4)_2SO_4$ gave poor growth of barley unless it was accompanied by $CaHPO_4$, in which case growth was about as good as when $Ca(NO_3)_2$, $NaNO_3$ or NH_4NO_3 was used with $CaHPO_4$. Prianschnikow's best growth of this plant occurred when $Ca(NO_3)_2$ and the phosphate were used together. Nehring (105) grew barley to maturity in unrenewed sand cultures with different H-ion concentrations, using several different compounds as nitrogen source. Judged by grain weight, optimal yields were obtained with $(NH_4)_2SO_4$ and with $Ca(NO_3)_2$, which were practically alike, while $NaNO_3$, urea, and the other

nitrogen compounds tested were sub-optimal. With a p_H value of 5, $(\text{NH}_4)_2\text{SO}_4$ and $\text{Ca}(\text{NO}_3)_2$ were equally effective, but the nitrate led to better yields with p_H values of 6 and 7 while the NH_4 salt was superior when the p_H value was 8. The best yield for NaNO_3 was obtained with p_H value of 5 and the best for urea was obtained with p_H value of 7. In sand cultures of barley, without washing or renewal of the solution, Pirschle (120, 121) found NH_4 inferior to NO_3 for a wide range of initial p_H values of the solution, but these two sources of N were about equally effective when the sand was subjected to frequent washing and renewal of the solution and when the p_H value of the solution was 7.0, 8.0 or 9.0. When the p_H value was below 7.0, NO_3 was superior to NH_4 , even with frequent washing and renewal of the solution.

Summarizing the results obtained with barley, no one appears to have recorded any experiments in which NH_4 was found to be definitely superior to NO_3 for the growth of barley, but NH_4 has apparently equalled NO_3 in effectiveness when the experimental conditions other than nitrogen supply were suitable. It seems that growth of barley might be retarded by relatively high acidity resulting indirectly from the use of ammonium salts in the nutrient medium and that NH_4 might not be a suitable source of N for this plant unless experimental conditions prevented the development of excessive H-ion concentration or antagonized the toxic effect of acidity in some way. Ammonium nitrate seems to have been a suitable source of N for barley in experiments in which that salt has been tested.

English rye grass (Lolium perenne)

Pirschle's tests (119) indicated that NO_3 was superior to NH_4 for the nitrogen nutrition of English rye grass.

Maize (Zea Mays)

Among the earliest experimenters on the ammonium nutrition of maize was Hampe (48, 49, 50, 51), who employed solution cultures. He found that this plant grew well with N supplied as NO_3 but concluded that NH_4 of inorganic salts was absorbed and assimilated if the harmful effects of the acidity resulting from its absorption were not allowed to become too pronounced. He found urea superior to uric acid and glycocoll as good as nitrates for his maize plants. Kühn (80) also reached the conclusion that maize could assimilate NH_4 in solution cultures. His plants grown with NO_3 as the only source of N failed to mature but those supplied only with ammonium phosphate or with $(\text{NH}_4)_2\text{SO}_4$ reached maturity. Wagner (161) reported that young maize plants did not thrive when N was supplied as ammonium phosphate. Ammonium carbonate gave poor growth but its injurious effect was much less pronounced when the culture solution was kept nearly saturated with CO_2 . He thought that glycine and creatine were absorbed and assimilated by maize. The conclusion that NH_4 was assimilated by this plant was also reached by Muntz (101), but Mazé (94, 95) thought that nitrification had occurred in Muntz's cultures supplied with NH_4 as the only source of N. However, when Mazé repeated Muntz's experiments the results were similar to those reported by the latter. Mazé came to the conclusion that NH_4 was as good as NO_3 if the N concentration were kept relatively low. He also noted that maize in advanced stages of development grew more rapidly with NO_3 than with NH_4 . Gerlach and Vögel (41) carried out what appear to have been very careful tests with sterilized-solution cultures of maize, obtaining just as good growth with NH_4 as with NO_3 . Perotti (114) also agreed

that NH_4 was directly assimilable by this plant. Lehmann (82) found that young maize plants gave better growth with NH_4 than with NO_3 but as his plants became larger and older NO_3 was superior. Direct assimilation of NH_4 by maize was confirmed by Kalinkin (67). With sterilized-sand cultures Schulow (142, 143) obtained better growth of maize with NH_4NO_3 than with $\text{Ca}(\text{NO}_3)_2$, in the presence of KH_2PO_4 , but his best results with the phosphate were secured with asparagin as source of N.—Rautenberg and Kühn (134) failed to obtain good growth of maize with NH_4 as the only source of N but NH_4NO_3 gave larger yields than were obtained with NO_3 alone. Graftiau (42) furnished additional evidence supporting the conclusion that NH_4 was directly assimilated by maize, without previous transformation. That different varieties of maize showed different relations to NO_3 and NH_4 was reported by Brigham (19); pop-corn appeared to prefer NO_3 to NH_4 but dent corn grew better with N supplied as NH_4 . With *Bacillus subtilis* in the culture medium, urea, asparagin and alanine each gave some very good yields in Brigham's maize experiments. Prianischnikow (128) obtained better growth of maize with NH_4Cl (along with CaCO_3) than with $\text{Ca}(\text{NO}_3)_2$. In another paper (131) the same writer says that Dikussar had found, for maize as well as for sugar beet, that NH_4 was superior to NO_3 when the p_{H} value of the medium was 7.0, while NO_3 was superior when the p_{H} value was 5.5. Mevius (97), using solution cultures, gave special attention to the question of the "physiological acidity" of ammonium salts and the influence of CaCO_3 , aeration, and other factors in counteracting it. In general, his largest yields of maize were obtained with NH_4NO_3 , and NH_4 alone was superior to NO_3 alone only when low concentrations were employed. Loo (87,

88), using solution cultures, obtained greater maize yields with NaNO_3 than with NH_4Cl or $(\text{NH}_4)_2\text{SO}_4$. Ammonium nitrate and $(\text{NH}_4)_2\text{HPO}_4$ gave yields as good as NaNO_3 in some tests but other tests showed them to be inferior to NaNO_3 . Allison's (2) solution cultures gave somewhat greater weight yields with $(\text{NH}_4)_2\text{SO}_4$ than with NaNO_3 but use of these two salts together gave greater yields than were obtained with $(\text{NH}_4)_2\text{SO}_4$ alone. Pirschle's (119, 120, 121, 122) solution cultures with unrenewed solutions showed NO_3 superior to NH_4 for maize. Four experiments with continuously flowing solutions showed superiority of NH_4 to NO_3 when the p_{H} value was 5.8. With p_{H} value of 5.0, 6.0, 7.0, or 7.1 yields with NO_3 and NH_4 were about alike and NO_3 was superior when the p_{H} value was below 5.0 or above 7.0. Similar results were obtained in an additional experiment with continuous flow of solution, but in this the optimal yields were obtained when both NO_3 and NH_4 were present, as NH_4NO_3 . In the acid range of p_{H} values the last-named salt gave better growth than was given by the use of NO_3 alone. In Pirschle's most recent experiment (122) the similarity of NH_4 and NO_3 was extended far into the alkaline range of p_{H} values, as far as 8.0.

Summarizing the results of culture experiments on the nitrogen nutrition of maize, good growth has been obtained in many instances when NH_4 was the only source of N and NH_4 has been found superior to NO_3 in some cases. Ammonium seems to have given about as good growth as was obtained with NO_3 when the nutrient medium was not too acid and especially when the N content of the medium was relatively low. Different varieties and different stages of development of the plants appeared to show different relations to NO_3 and NH_4 . Am-

monium nitrate, which supplies both NO_3 and NH_4 together, gave better growth than was given by either NO_3 or NH_4 alone.

Millet (Setaria)

Ehrenberg (32) reported that NO_3 was superior to NH_4 as source of N for sugar millet.

Oats (Avena sativa)

As early as 1859 Knop (71) published a report on soil-pot experiments concluding that NaNO_3 and NH_4NO_3 were equally beneficial to oats, but that urea, hippuric acid and some other organic nitrogen compounds were not suited to this plant. Birner and Lucanus (15) concluded that NO_3 could not be replaced by NH_4 for oats, and Bener (13, 14) also failed to obtain good growth of this plant with NH_4 as source of N. Pitsch (123) compared NO_3 with NH_4 in experiments with oats and found the nitrate to be decidedly superior. Clausen (20) obtained better growth of this plant with $(\text{NH}_4)_2\text{SO}_4$ than with NaNO_3 but he was inclined to attribute this result to characteristics of the soil used. Of Krüger's (79) three experiments with oats, one showed NH_4 and NO_3 to be equally effective, another showed NH_4 to be superior and a third showed NO_3 to be superior. As for barley, so also for oats, this writer considered NO_3 and NH_4 as about equally good. Ehrenberg (31) failed to obtain good growth of oats with NH_4 . While Prianischnikow (124, 130) found NH_4 inferior to NO_3 for oats, the former was apparently assimilated to some extent under some conditions; nitrate gave the best growth. From his sterilized-solution cultures Schulow (143) concluded that both NH_4 and NO_3 were suitable for oats in early growth phases but that NO_3 was a better source of N when the plants were

more advanced. Pfeiffer, Hepner and Frank (117) found NO_3 superior to NH_4 for this plant. In the sand-culture experiments of Pirschle (119, 121) optimal weight yields of oats were obtained with NO_3 , whether or not the sand was frequently washed, with renewal of the solution. In one experiment NH_4 gave some yields about as good as were obtained with NO_3 , but only with solutions having p_H values as high as 7.0, 8.0, or 9.0. The best yield was with NO_3 and a p_H value of 5.0. In Pirschle's solution cultures, with continuous flow as well as without renewal, oats grew best with NO_3 as source of N. In later experiments Pirschle (120, 122) obtained about as good growth with NH_4 as with NO_3 when the p_H value of the solution was 6.0.

Summarizing the results on oats, the effectiveness of NO_3 as N source appears to have been closely approached by NH_4 in only a few instances and no report has been found in which NH_4 is shown to have been superior to NO_3 for this plant. The effectiveness of NH_4 seems to have depended on the H-ion concentration of the medium, probably also on other features. Oats appears to be much like barley in this respect.

Rice (Oryza sativa)

Readers who are specially interested in rice will find Kondo and Isshiki's recent bibliography (72) a very valuable aid. The study of the nitrogen relations of this plant seems to have begun with Kellner (70), who published in 1884. From experiments with solution cultures they concluded that both NO_3 and NH_4 were assimilated by this plant, but NH_4 gave best results with young plants while older plants grew better with NO_3 as source of N. In general, their best results were obtained when both of these sources of N were supplied together, as NH_4NO_3 .

Nagaoka (103) found NH_4 superior to NO_3 , confirming a similar conclusion of Daikukara and T. Imasaki (24). Aso and Bahadur (6) agreed with Nagaoka and went so far as to regard NaNO_3 as unsuitable for rice. Pantanelli and Severini (108) found, in sterilized-solution cultures, that NaNO_3 gave better growth than was given by NH_4Cl , about as good growth as was given by NH_4NO_3 or $(\text{NH}_4)_2\text{SO}_4$, but optimal yields were obtained when they used $(\text{NH}_4)_3\text{PO}_4$ or NH_4MgPO_4 as source of N. Krauss (77, 78) concluded, from soil-pot and field tests, that ammoniacal nitrogen was specially suitable as nitrogen source for rice. Perciabosco and Rosso (115) found that rice was peculiarly sensitive to nitrite poisoning. Kelley (68, 69), working in Hawaii, wrote that $(\text{NH}_4)_2\text{SO}_4$ led to "considerable increases in yield of straw and grain of rice, while nitrate of soda was ineffective." Harrison (53) found that NO_3 was effective on rice paddies while ammonium gave good results. Trelease and Paulino (156), working at Los Baños, employed pots of solution-saturated soil and studied the salt nutrition of rice by the method of triangular diagrams, which had been introduced by Schreiner and Skinner (139, 140), Tottingham (153) and others. Best yields of straw and grain were obtained with $(\text{NH}_4)_2\text{SO}_4$ but NH_4NO_3 was nearly as effective as the sulphate. Sodium nitrate and $\text{Ca}(\text{NO}_3)_2$ gave much less satisfactory growth. Espino (33) employed solution cultures of young rice plants on a rotating table in the greenhouse of the Johns Hopkins University, at Baltimore, and used the triangular diagram in choosing sets of salt proportions that would represent a wide range of logical possibilities. His best growth was obtained with NH_4NO_3 ; when NO_3 was the only source of N growth was only fair; when the

source of N was NH_4 alone the best sets of salt proportions gave dry yields nearly as large as were obtained with NH_4NO_3 but what was taken as "ammonium injury" to the foliage was then present. Willis and Carrero (163) also held that nitrates were less suitable than ammoniacal nitrogen for rice. Loo (87, 88) compared $(\text{NH}_4)_2\text{SO}_4$, NaNO_3 , NH_4HPO_4 and NH_4NO_3 , and took the H-ion concentration of his solutions into account. In one test $(\text{NH}_4)_2\text{SO}_4$ gave largest yields and the three remaining salts gave good yields that were about alike. In another test yields from all four salts were good and nearly alike. Very poor growth was obtained with NH_4HCO_3 as source of N. Bartholomew (9) obtained better rice yields with $(\text{NH}_4)_2\text{SO}_4$ and with some organic nitrogenous fertilizers than with NaNO_3 . Palisoc (106) found, with solution cultures, that NH_4NO_3 was greatly superior to $(\text{NH}_4)_2\text{SO}_4$, while $\text{NH}_4\text{H}_2\text{PO}_4$ led to poor growth. Fukaki's (38) solution-culture experiments with rice showed $(\text{NH}_4)_2\text{SO}_4$ as better than $\text{Ca}(\text{NO}_3)_2$ for vegetative development, but these nitrogen sources were about equally effective for seed production and $\text{Ca}(\text{NO}_3)_2$ was somewhat more favorable for seed maturation. Espino and Estioko (35) found that NH_4 was superior to NO_3 for young rice plants, but they held that some NO_3 was essential to healthy foliage and concluded that both NO_3 and NH_4 were required in cultures of rice when young. Pirschle's (121) sand cultures of this plant, with frequent washing and renewal of the solution, gave optimal dry-weight yields when N was supplied as NH_4 , but NO_3 was superior to NH_4 in his cultures without renewal of solution. With regard to H-ion concentration of the medium, NH_4 was superior to NO_3 when the p_{H} value of the solution was 6.8, 7.0 or 8.0, but NH_4 was inferior when the p_{H}

value was 3.0, or 4.0. Pirschle's experiments with continuous flow of solution (122) showed as good yields with NH_4 as with NO_3 , but NH_4 was superior when the p_{H} value of the solution was 5.0, 6.0 or 7.0 and the yields were about alike when the solution had a p_{H} value of 8.0 or 9.0. The best yields of all were obtained when N was supplied as urea or when NH_4 and NO_3 were supplied together, either as separate salts or as NH_4NO_3 .

Summarizing the experimental evidence for rice, it seems safe to conclude that this plant has generally grown better with NH_4 than with NO_3 as source of N, in cultures as well as in paddy-field experiments. But some cultures gave equally good results with either NH_4 or NO_3 and in some instances NO_3 appeared to be somewhat superior to NH_4 . Rice appears to have shown less sensitiveness to "physiological acidity" than most of the other plants whose nitrogen nutrition has been experimented upon. There seems to be no doubt that this plant is able to assimilate both NO_3 and NH_4 and some writers think that both of these ions are essential to excellent growth and healthy foliage. Ammonium nitrate has given very good results with rice.

Rye (Secale cereale)

Pirschle's experiments (121) with rye showed this plant to be much like oats and barley, generally showing optimal yields with NO_3 as source of N, with similar relations to the H-ion concentration of the medium. The ammonium ion seems generally to have been unsuitable as the only source of N for this plant.

Sorghum (Holcus sorghum)

Pirschle's (121) solution cultures with unrenewed solutions showed NO_3 to be superior to NH_4 as source of N for sor-

ghum. When the solutions were renewed continuously NH_4 gave the largest weight yields with p_{H} value of 5.0 or 6.0, but NO_3 gave largest yields with lower or with higher p_{H} values. The writer of the present review has recently carried out a series of solution-culture experiments on sorghum, in the greenhouse of the Johns Hopkins Laboratory of Plant Physiology. The results of these tests, which have not yet been published, show that best growth was obtained when N was supplied as $\text{Ca}(\text{NO}_3)_2$ but NH_4NO_3 gave nearly as good growth. Fair growth was obtained with $(\text{NH}_4)_2\text{SO}_4$ as the only source of N. It appears that these sorghum plants were able to assimilate some of their required N as NH_4 but that their preference was for NO_3 .

Sugar Cane (Saccharum)

McGeorge's (96) sand-culture tests gave good growth of sugar cane with N supplied as NO_3 but not when NH_4 was the only source of N. Van den Honert (59) found that NH_4 gave poor growth of sugar cane and attributed this to a characteristic root injury, which appeared in his NH_4 cultures. He recalled that Miss G. Wilbrink had previously observed a similar root injury in cane plants that had been subjected to the influence of ammonium salts. In Pardo's (110) preliminary solution-culture tests NaNO_3 was a very effective source of N for sugar cane. Urea gave fair results but cultures with $(\text{NH}_4)_2\text{CO}_3$, with certain amino acids or with guanidine as source of N showed very poor growth. Additional experiments by the same writer (111) indicated that $(\text{NH}_4)_2\text{SO}_4$, NH_4NO_3 and urea were decidedly inferior to $\text{Ca}(\text{NO}_3)_2$ for young cane plants but that older plants (after 20 or 32 weeks of solution culture) grew better with NH_4NO_3 than with $\text{Ca}(\text{NO}_3)_2$ as source of N. Considerable experimen-

tal evidence favors the tentative conclusion that sugar cane prefers NO_3 in its earlier phases of development but that NH_4 may be superior to NO_3 when the plants are more advanced.

Wheat (Triticum sativum)

Mayer (92), who published in 1874, thought that wheat might assimilate NH_4HCO_3 when absorbed through the foliage. Ville (159) found, as with barley, that NH_4Cl and some organic nitrogen compounds gave good growth of wheat, but he did not include nitrates in his tests. Pitsch's (123) pot experiments with sterilized soil included winter and spring wheat as well as barley and oats and he obtained better growth of wheat with NaNO_3 than with $(\text{NH}_4)_2\text{SO}_4$, just as in the case of the other two cereals. However, some of his tests with winter wheat showed $(\text{NH}_4)_2\text{SO}_4$ to be nearly as effective as NaNO_3 . Pfeiffer, Hepner and Frank (117) found NaNO_3 to give better growth of wheat in sand cultures than was given by either $(\text{NH}_4)_2\text{SO}_4$ or NH_4NO_3 , the latter being somewhat the better of these two ammonium salts. Perotti (114) obtained good growth of wheat in soil cultures with NH_4NO_3 and with $\text{Ca}(\text{CN})_2$. Hutchinson and Miller (63), who used sterilized-sand cultures as well as solution cultures, found that NaNO_3 gave much better growth of this plant than was given by $(\text{NH}_4)_2\text{SO}_4$ but that when the latter salt was applied with CaCO_3 it gave about as good growth as was given by NaNO_3 . With sterilized solutions Pantanelli and Severini (108) found NaNO_3 to be a better source of N for wheat than either NH_4Cl or $(\text{NH}_4)_2\text{SO}_4$, but $(\text{NH}_4)_3\text{PO}_4$ or NH_4MgPO_4 led to yields several times as large as were obtained with NaNO_3 . In sterilized-sand cultures these same authors (109) found that KNO_3 gave better results than were

obtained with either $(\text{NH}_4)_3\text{PO}_4$ or NH_4MgPO_4 . Several organic salts of NH_4 were also tried, as well as phosphates. These writers concluded that the injurious influence of NH_4 salts of strong acids might be avoided through the use of NH_4 salts of weak acids. Loo's (87, 88) solution cultures of this plant gave about as good growth with NH_4HPO_4 as with NaNO_3 , perhaps because the phosphate did not give rise to such high H-ion concentration as is apt to result from the use of $(\text{NH}_4)_2\text{SO}_4$ or NH_4Cl . Pirschle (119, 121) included wheat in his sand-culture experiments, with and without frequent washing and renewal of the solution, and found NH_4 and NO_3 about equally good when the p_{H} value of the solution was 3.0, 7.0 or 9.0; when the p_{H} value was 6.0 or 8.0, however, NH_4 led to the better growth and when the p_{H} value was 4.0 or 5.0, NH_4 was inferior to NO_3 . In solution cultures, with continuous flow as well as with unrenewed solutions, Pirschle obtained better growth of wheat with NO_3 than with NH_4 . Further experiments (120, 122) gave nearly the same optimal yields with NH_4 and with NO_3 but NH_4 was somewhat superior for p_{H} values from 6.0 to 9.0, while NO_3 was somewhat superior when the p_{H} value of the solution was below 6.0.

Summarizing, for wheat, NH_4 appears to have been about as suitable as NO_3 , or even superior to it under some conditions. It again appears that the H-ion concentration of the medium may directly or indirectly influence the relative effectiveness of these two sources of N.

Summary for Gramineae

It appears that all the Gramineae tested were capable of deriving at least a portion of their needed N from NH_4 as well as from NO_3 , but that the use of NH_4 as the only source of N has sometimes appar-

ently resulted in secondary conditions that were more or less injurious to the plants, notably high H-ion concentration of the medium. Different plant forms appear to differ in regard to their capacity to thrive with NH_4 as the only source of N and different varieties of the same species, as well as different developmental phases of the same form, have shown marked differences in this regard. The total concentration of the nutrient solution used and the partial concentrations of its component compounds (including the source or sources of N) appear to have exerted influences, either through resultant high H-ion concentration or otherwise, upon the apparent effectiveness of NH_4 and NO_3 as sources of N. Frequency of renewal of nutrient solutions has also been influential, as should be expected, since the composition of a solution in cultures without adequate renewal is subject to more or less rapid alteration through differential absorption by the plants.

Definite conclusions as to the relative capacities or nitrogen preferences of these different plant forms are not yet permissible, but it may be said that rice has greatly surpassed the other Gramineae tested, with respect to its tolerance of such injurious or retarding influences as may have resulted from the employment of NH_4 as sole nitrogen source. Under the various conditions of the experiments that have been carried out, rice has generally seemed to prefer ammoniacal N to nitrate N but it has grown better with NH_4NO_3 than with NH_4 alone as source of N. Maize and wheat appear to have grown about as well with NH_4 as with NO_3 , under suitable conditions, but different sets of experimental conditions seem to have swung the apparent nitrogen preference to one or the other of these two sources; sometimes one was somewhat superior and sometimes the other. Maize has

given better growth with NH_4NO_3 than with either NH_4 or NO_3 alone. Sorghum appears to have preferred NO_3 to NH_4 although the latter gave fair growth in some tests and good growth resulted from the use of NH_4NO_3 . Sugar cane seems to have preferred NO_3 to NH_4 in early phases of development, while NH_4 or NH_4 and NO_3 together (NH_4NO_3) were superior to NO_3 alone in more nearly mature phases. Barley, oats and rye have generally given poor growth when N was supplied only as NH_4 , while NO_3 generally gave very good growth. In no case did either of these three plant forms show superiority of NH_4 ; they seem to have been more sensitive to acidity of the medium than were any of the other Gramineae for which experiments have been reported. Barley has given good growth with NH_4NO_3 as double source of N. The use of this double source led, in some tests, to better growth than was given by either NH_4 or NO_3 alone, for rice, maize and the more advanced phases of sugar cane.

HYDROCHARITACEAE

Pirschle's (121) tests appear to indicate that NO_3 was more favorable than NH_4 for the submerged aquatic, *Elodea canadensis*, excepting when the medium had p_{H} value of 5.0, when NH_4 was superior to NO_3 .

LEGUMINOSEAE

It is well known that legumes are able to obtain most, if not all, of their nitrogen requirements through symbiosis with nodule-forming bacteria when these are present, but it is also true that nitrogen compounds may be absorbed from the soil by these plants. The relations of leguminous plants to nitrogen compounds in the medium about the roots are especially difficult to study, since not only the nitro-

gen bacteria of the soil but also the symbionts need to be excluded from experimental cultures, or else taken quantitatively into account. For convenience, the notes of this section will be presented in a series of subsections representing the several plant forms considered.

Bean (Phaseolus vulgaris, P. multiflorus)

As early as 1842 de Saussure (137) reported that bean plants in sterilized sand were able to obtain their needed N from NH_4NO_3 . Rautenberg and Kühn (134) reached the same conclusion, finding that NH_4NO_3 , in solution cultures, gave better growth than was obtained when NO_3 was the only source of N. The use of NH_4 as the only source of N gave poor growth, but it led to a somewhat greater yield of seed than was obtained when NH_4NO_3 was used. Griffiths (44), growing young bean plants in sterilized solutions, found that they thrive with $(\text{NH}_4)_2\text{SO}_4$ as the only source of N. With cultures of bean in sterilized and in unsterilized soil, Pitsch (123) obtained generally better growth and earlier ripening of seed when N was supplied as NO_3 than when NH_4 was the only nitrogen source. Nodules were plentiful on the roots of the plants in unsterilized soil but were not present when the soil had been sterilized. Loo (87, 88) found, with solution cultures of this plant, that NaNO_3 was superior to NH_4NO_3 , NH_4Cl and $(\text{NH}_4)_2\text{SO}_4$; but NH_4HPO_4 led to as good growth as was obtained with NaNO_3 . In Pirschle's (119, 120, 121) solution cultures, both without renewal and with continuous flow, scarlet-runner bean (*Phaseolus multiflorus*) generally gave greater dry weights with NO_3 than with NH_4 , but in one series of tests with continuous flow these two sources of N were about equally effective. Pirschle's scarlet-runner bean plants did not appear to be very sensitive to differ-

ences in H-ion concentration, but continuous-flow cultures gave greatest dry weights with $(\text{NH}_4)_2\text{SO}_4$ when the p_{H} value of the solution was 6.0, the weights being smaller when the p_{H} value was lower or higher.

Pea (Pisum sativum)

Ehrenberg (31) cites Hosäus (60, 61, 62) as having shown that pea thrive as well when supplied with NH_4 as when furnished with NO_3 as its source of N. Mazé (94) found with sterilized-solution cultures that pea grew very well when supplied with N only in the ammoniacal form. In Kossowitsch's (74) sterilized-sand cultures this plant gave good growth with N supplied as either $\text{Ca}(\text{NO}_3)_2$ or $(\text{NH}_4)_2\text{SO}_4$. Prianischnikow (129) obtained good growth of pea in sand cultures with NH_4HCO_3 as nitrogen source, better than with NH_4Cl . Hutchinson and Miller (63, 64) studied the nitrogen nutrition of pea with special precautions to avoid nitrifying bacteria, reporting that NaNO_3 and $(\text{NH}_4)_2\text{SO}_4$ gave good and approximately equal dry weights; some amino compounds gave better yields than were obtained with $(\text{NH}_4)_2\text{SO}_4$. Zaleski and Tutorski (165) obtained better growth of pea seedlings with NO_3 than with an ammonium phosphate, but sodium aspartate led to as good development as was obtained with NO_3 . Schulow (142) obtained better growth of pea with $\text{Ca}(\text{NO}_3)_2$ than with NH_4NO_3 . As in the case of bean, Loo's (87, 88) experiments with pea showed NaNO_3 superior to $(\text{NH}_4)_2\text{SO}_4$, NH_4Cl or NH_4NO_3 , but NH_4HPO_4 was as good as NaNO_3 . In Pirschle's (119, 120, 121, 122) experiments, pea gave better growth with NO_3 than with NH_4 , whether the nutrient medium was continuously renewed or remained unchanged, and for a wide range of p_{H} values.

Vetch (Vicia)

In Mazé's (94) sterilized-solution cultures he found, for vetch as well as for pea, that NH_4 and NO_3 both led to good growth, being about alike. Prianschnikow (126) found, in sand-culture experiments, that vetch grew about equally well with either $\text{Ca}(\text{NO}_3)_2$, NaNO_3 or NH_4NO_3 , but failed when N was supplied as $(\text{NH}_4)_2\text{SO}_4$. As for bean and pea, so also for vetch, Loo's (87, 88) solution cultures gave better growth with NaNO_3 than with NH_4NO_3 , NH_4Cl or $(\text{NH}_4)_2\text{SO}_4$. Pirschle's (119, 121) results for vetch were also like those for bean and pea, NO_3 being superior to NH_4 for a wide range of p_H values. Windsor bean (*Vicia faba*), however, gave as good growth with NH_4 as with NO_3 , when the p_H value of the solution was 5.0 or 6.0.

Lupines (Lupinus luteus, L. angustifolius, L. albus)

Lehmann (82) reported experiments with yellow lupine grown in sterilized sand, in which NaNO_3 gave much better growth than was obtained with $(\text{NH}_4)_2\text{SO}_4$. The seed yield was greater, however, from the plants supplied with the ammonium salt, in which case symbiotic bacteria were probably present, supplying fixed nitrogen derived from the air. Prianschnikow's (129) results with lupine in sand cultures showed that $\text{Ca}(\text{NO}_3)_2$, NaNO_3 and NH_4NO_3 were highly and about equally effective but $(\text{NH}_4)_2\text{SO}_4$ failed to give even fair growth. Loo's (87, 88) solution cultures of lupine showed that NH_4NO_3 was effective as nitrogen source and about equal to NaNO_3 . In solution cultures, with continuous flow as well as without solution renewal, Pirschle (119, 121) obtained optimal yields of yellow lupine with NO_3 but NH_4 was also effective and it equalled NO_3 when the p_H value of the solution was 3.2, 4.5, 7.1 or 8.4.

In sand cultures of blue lupine, with frequent washing and renewal of the solutions, the same author found that NO_3 was superior to NH_4 , with a p_H value of 4.5 or 8.4, but NH_4 was about as effective as NO_3 when the p_H value of the solution used was 3.2, 5.8, or 7.1. The very best yields were obtained with NO_3 .

Clover (Trifolium)

Knop (71) reported that clover was able to thrive in pots of soil supplied with NH_4 , while hippuric acid and urea affected the plants injuriously.

Alfalfa (Medicago sativa)

Pirschle's tests (119, 120, 121) with alfalfa gave better growth with NO_3 than with NH_4 .

Soy-bean (Glycine hispida)

Shive (144) found that NH_4 salts were toxic to soy-bean in solution culture. Wolkoff (164) obtained better growth of soy-bean in solution cultures with $(\text{NH}_4)_2\text{SO}_4$ and $\text{Ca}(\text{NO}_3)_2$ applied together than when KNO_3 was applied with $\text{Ca}(\text{NO}_3)_2$. In Pirschle's (119, 121) sand-culture tests NO_3 gave better growth than was given by NH_4 , but other experiments indicated that this plant might do equally well with NH_4 as source of N if the effects of "physiological acidity" were avoided, as by means of solution cultures with continuous flow. When acidification was prevented in solution cultures NH_4 proved superior to NO_3 if the p_H value of the solution was 6.0 or 8.0. Tiedjens and Robbins (150) grew soy-bean plants in sand cultures with N supplied as $(\text{NH}_4)_2\text{SO}_4$ or as NH_4OH and with a p_H value of 7.0–8.8. Both of these sources of N gave very good growth, being equal or superior to $\text{Ca}(\text{NO}_3)_2$, but the sulphate was surpassed by the hydroxide.

Sensitive Plant (Mimosa pudica)

Bouchardat (16) placed cuttings of sensitive plant in solutions for rooting and observed that those in solutions containing NH_4 failed to develop.

Summary for Leguminosae

It appears that leguminous plants have been generally found to be capable of absorbing and assimilating NH_4 as well as NO_3 . Bean and lupine generally seem to have preferred NO_3 to NH_4 as source of N, when NH_4 was supplied as salts of strong acids. For pea, some experiments have shown NO_3 to be superior to NH_4 and other experiments indicated that these two ions were about equally effective. Soy-bean seems to have been more susceptible than bean, lupine or pea to the physiological acidity resulting from the presence of NH_4 salts of strong acids, but nevertheless this plant seems to have been better suited to NH_4 nutrition than either of the other forms just mentioned.

With the exception of soy-bean in some experiments, none of the legumes tested appears to have given as large yields with NH_4 (and any tested p_H values) as were obtained with NO_3 when the p_H value of the solution was optimal for growth with NO_3 . These plants seem to have been generally shown to be more or less unsuited to NH_4 and when both NH_4 and NO_3 were supplied together growth was not better than with NO_3 alone.

LILIACEAE

Aso and Behadur (6) obtained much better growth of onion (*Allium cepa*) when N was supplied as $(\text{NH}_4)_2\text{SO}_4$ than when it was supplied as NaNO_3 .

LINACEAE

In Pantanelli and Severini's (108) experiments flax (*Linum usitatissimum*) showed as good growth with NH_4Cl ,

$(\text{NH}_4)_2\text{SO}_4$ or NH_4NO_3 as was obtained when N was supplied as NaNO_3 . Ammonium tartrate gave optimal yields and NH_4HPO_4 was inferior to each of the first three salts mentioned. Pirschle (121) obtained equally good growth of flax with NH_4 and with NO_3 when his nutrient solutions were not renewed, but with continuously flowing solutions and a p_H value of 6.0, NH_4 gave better growth than was given by NO_3 . These two ions were equally good when the flowing solutions had a p_H value of 4.0, 8.0 or 9.0.

MALVACEAE

In experiments on cotton (*Gossypium*), Holley, Pickett and Dulin (57) found that KNO_3 gave larger dry-weight yields than were obtained when N was supplied only as $(\text{NH}_4)_2\text{SO}_4$. Tiedjens and Robbins (150), using sand cultures of cotton, compared $(\text{NH}_4)_2\text{SO}_4$ and NH_4OH with $\text{Ca}(\text{NO}_3)_2$, finding that NH_4 gave as good growth as was given by the nitrate. Ammonium hydroxide led to even more vigorous growth than was obtained with the sulphate and no ammonium toxicity was observed. Best growth occurred with NH_4 when the p_H value of the medium was about 7.5 or 8.0. The disagreement between these results and those reported by Holley, Pickett and Dulin may be due to differences in the H-ion concentration of the solutions used. Naftel (102) has recently stated that his solution cultures and sand cultures of cotton showed that NH_4 and NO_3 together gave better growth than was given by either NH_4 or NO_3 as sole source of N; fruiting was earlier and more fruits were borne when both NH_4 and NO_3 were supplied together. Friedmann (37) appears to have carried out culture experiments with cotton using continuously flowing solutions with various H-ion concentrations. He employed $(\text{NH}_4)_2\text{SO}_4$, NH_4OH and KNO_3 . Results

were to be reported in a later paper, which has not been seen by the writer.

MUSACEAE

Espino and Viado (34) found, with solution cultures of abaca (*Musa textilis*), that $(\text{NH}_4)_2\text{SO}_4$ was "a far better source of nitrogen" than NaNO_3 .

POLYGONACEAE

Buckwheat (*Fagopyrum esculentum*) was found by Lehmann (82) to prefer NO_3 to NH_4 , but Ville (158) obtained good growth of this plant when N was supplied only as NH_4Cl or as organic compounds. Pirschle (120, 121) found NO_3 superior to NH_4 for a broad range of p_{H} values of the medium.

ROSACEAE

Davis's (26) experiments with two-year old apple trees (*Malus malus*) in pots of sand showed no significant fertilizer effects of either $(\text{NH}_4)_2\text{SO}_4$ or $\text{Ca}(\text{CN})_2$, whether the solution used had been sterilized or not, but markedly improved growth followed the application of NaNO_3 . Tiedjens and Robbins (150) experimented with year-old apple trees grown in sand cultures in which they had been allowed to suffer from nitrogen deficiency, which gave yellow leaves. One group was treated with nutrient solution in which N was supplied as $\text{Ca}(\text{NO}_3)_2$ alone and another group received N only in the form of $(\text{NH}_4)_2\text{SO}_4$. Both solutions had a p_{H} value of 5.4. The foliage of the NH_4 plants remained yellow but that of the NO_3 plants became green. But complete recovery of the NH_4 plants occurred when the p_{H} value of the solution used was 8.0. In the same paper these authors state that the foliage of peach seedlings in sand culture was yellow when N was supplied

only as $(\text{NH}_4)_2\text{SO}_4$ with p_{H} value of 5.4, but the leaves became green subsequently, after the p_{H} value had been changed to 8.0.

SOLANACEAE

Potato (*Solanum tuberosum*) was the subject of early experiments by Bouchardat (17), who used boxes of soil. He failed to obtain increased yields with ammonium salts. Stohmann (148), who used solution cultures, reported better growth of potato when NH_4NO_3 and $\text{Ca}(\text{NO}_3)_2$ were applied together than when KNO_3 and $\text{Ca}(\text{NO}_3)_2$ were applied together. Krüger (79) concluded, from soil-sand cultures, that this plant preferred NH_4 to NO_3 , as source of N. His conclusion may refer to yield of tubers only, for his total-weight data show NH_4 superior in one test and NO_3 superior in another test and his results differ with respect to the concentrations employed. It apparently made no difference whether the soil-sand mixture had been sterilized or not.

Tobacco (*Nicotiana tabacum*), in Lehmann's tests (82), was greatly benefited by NaNO_3 but $(\text{NH}_4)_2\text{SO}_4$ led to yields twice as large as were obtained with NaNO_3 . On the other hand, Pirschle (119) found that NO_3 was superior to NH_4 for tobacco. Wagner (162) reported that the burning quality of tobacco leaves was improved by the use of $(\text{NH}_4)_2\text{SO}_4$ as fertilizer but de Vries (160) thought that the burning quality was not influenced by fertilizer treatment. Using sterilized-solution cultures of tobacco Beaumont and his co-workers (11) reached the conclusion that nitrates were more readily assimilated than any of the other nitrogen sources tested; urea gave less satisfactory results, and NH_4 gave still poorer growth. They thought the unsuitability of NH_4 for tobacco might be only partially due to physiological acidity, as considered by

Prianischnikow (130), or to H-ion concentration, as considered by Mevius (97).

Tomato (*Lycopersicon esculentum*) was included in the sand-culture experiments of Tiedjens and Robbins (150), who compared $(\text{NH}_4)_2\text{SO}_4$ and NH_4OH with $\text{Ca}(\text{NO}_3)_2$ and found that NH_4 gave as good growth as was given by NO_3 . Ammonium hydroxide with p_{H} value of 7, 8 or 9 was especially satisfactory and no injurious effects due to NH_4 were observed. (See the photographs shown in figure 4 of the paper just cited.)

UMBELLIFERAE

According to Pfeiffer, Hepner and Frank (117), NaNO_3 was superior to NH_4NO_3 and the latter was superior to $(\text{NH}_4)_2\text{SO}_4$, for growth of carrot (*Daucus carota*).

IV. CONCLUSION

Although the review presented in this paper is not to be considered as complete, it is probably fairly representative of the technique and trend of investigation in this field. Many different forms of higher green plants have been studied by numerous experimenters. Experimental technique has been continually improved. Nevertheless, it is apparent that the results reported do not yet lead to satisfactory general conclusions. It appears that the NO_3 ion is a suitable source of nitrogen for higher green plants in general but many forms have been found to thrive with the NH_4 ion as sole nitrogen source. In some cases these two ions, when supplied separately, showed about the same degree of effectiveness; in some other cases NO_3 was superior to NH_4 , although the latter was nutritionally effective to a considerable extent; in a few cases NH_4 was found to be definitely superior to NO_3 ; and a good many tests indicated that NH_4NO_3 (which supplies both NH_4 and NO_3) was equal or superior to either one of these two ions

supplied separately. Not only have different kinds of plants been found to show marked differences in their capacity to thrive with NH_4 as the only source of nitrogen, but different experimenters have in many instances obtained very different results with the same kind of plant, and separate but similar tests of the same plant by the same investigator have led to discordant results in some instances. It seems clear that such disagreement must be related to experimental influences or conditions that have not as yet been adequately reckoned with. A number of conditions that may possibly be involved will readily suggest themselves.

Differences among different plant forms, with regard to their NH_4 and NO_3 relations, are very striking and disconcerting when one tries to summarize these relations for higher green plants in general. There seems to be no reason for doubting that species and varieties probably do differ greatly in this as well as in many other respects, but the plants studied cannot yet be classified according to their preferences in respect to nitrogen supply. The apparent differences indicated by the literature and reflected in this review are not to be taken as really very well established, however, since the many experiments dealt with are generally not truly comparable in any satisfactory sense. Relatively slight differences in experimental technique may possibly account for great differences in results, without the supposition that the various plant forms are really as different as they appear to be. It is of course essential that the plants used in any series of comparable tests should be as nearly alike as possible at the beginning for all tests and varieties and genetic strains, as well as species, need consideration if definite results are to be expected from comparative experiments. Furthermore, the preliminary treatment of

the plants used (as in seed germination, for example) needs to be standardized, lest different lots of plants of the same form may differ in physiological vigor. The developmental phase of the plants used appears to be of great importance; nutritional requirements for different developmental phases and different degrees of vigor may be very different for the same variety of plant. Germinating seeds, sprouting eyes (as of sugar cane or potato), young plants, older plants, mature plants, all of the same species and strain, may be expected to perform more or less differently when exposed to the same environmental complex. Since the plants of an experiment change as they become older the time factor is naturally a crucial variable; results obtained with a longer experiment period may be quite unlike those obtained with a shorter period, even if all experimental features excepting duration are closely similar in the two cases.

In many instances it is difficult or impossible to institute useful comparisons among the results obtained in several different experiments because of the employment of different criteria in judging growth and development. A great variety of plant criteria have been used by experimenters on plant nutrition and different criteria may indicate markedly different relations to nutritional conditions. Green weight, dry weight, height, transpiration, leaf area, color, branching, flowering, fruit production, tuber production, are examples. Grain production and straw production are often compared, as in agronomic studies on cereals. Quality of the product is sometimes considered as well as quantity, and this consideration introduces many special kinds of criteria. Earliness or promptness of flowering, fruiting, and other events in the life cycle are sometimes important considerations in nutrition experiments; thus, if two differ-

ent nutrient solutions are compared, with all other environmental influences alike, both may give sensibly the same result at the end of a sufficiently long experiment period, but flowering or fruiting may occur much earlier with one solution than with the other. Comparisons of growth vigor in different regions of the plant body may bring out important nutritional relations; for example, NH_4 has been found, in some of the writer's experiments, to give less root growth of sugar cane than was shown when nitrogen was supplied only as NO_3 , while NH_4 appeared to be superior for top growth. The ratio of tops to roots may be a useful criterion for comparing cultures with respect to growth in general; in some tests ammoniacal nitrogen led to much more vigorous tillering in sugar cane than was obtained with NO_3 .

Various special plant criteria refer to diseased conditions of the plants; for example, Tottingham's (153) magnesium injury to wheat foliage, which has recently been studied by Trelease and Trelease (157), and Espino's (33) ammonium injury to rice leaves. When diseased conditions occur they should naturally be taken into account, along with weight values or whatever general criteria are employed.

However species and varieties and different developmental stages of the same form may differ, there is certainly no doubt that the kind and degree of the nutritional response shown by any given plant species or variety toward any specified substance or ion is influenced not only by the nature and concentration of the substance or ion specially considered but also by concentrations and relative proportions of many other molecules and ions that are concomitantly present and effective in the nutrient medium. Hydrogen-ion concentration has recently been studied a great deal in connection with nitrogen nutrition and

other non-nitrogenous ions have received attention from some experimenters.

We may consider H-ion concentration for a useful illustration of the complications that became obvious as soon as non-nitrogen conditions are taken into account. Suppose that two fairly comparable series of satisfactory solution cultures have been simultaneously carried out with suitable plants, the sole nitrogen source being NO_3 for one series and NH_4 for the other. Also suppose that each series has included a number of different but maintained p_{H} values of the solution, ranging from 4.0 to 9.0. The results might show that the p_{H} value of the optimal solution of the NO_3 series is 6.0, with a growth index of 1.10, while the p_{H} value of the optimal solution of the NH_4 series might be 8.0, with a growth index of 1.00. This might lead to the conclusion that the plants used, under the general conditions of this hypothetical series of experiments, had apparently preferred NO_3 to NH_4 as source of nitrogen, for the greatest growth index is shown for NO_3 ; but it would be noted that the best solution with NH_4 led to almost as good growth as was given by the best solution with NO_3 . Such a conclusion would be based on the more general optima, without reference to p_{H} value, but a quite different conclusion might be reached if comparisons were instituted in the other direction, each two solutions with the same H-ion concentration being compared. For example, with p_{H} value of 6.0 the hypothetical growth indices for NO_3 and NH_4 might be respectively 1.10 and 0.80; and with p_{H} value of 8.0 the corresponding indices might be 0.80 and 1.00 respectively. From the first comparison (with p_{H} value of 6.0) NO_3 would appear to have been preferred to NH_4 , but the second comparison (with p_{H} value of 8.0) would lead to the opposite conclusion. A study of the complete double series might lead to the gen-

eralization that NO_3 appeared to have been superior to NH_4 with suitably acid solutions but that NH_4 appeared to have been superior to NO_3 with suitably alkaline solutions.

Different plant forms have been found to differ in their preferences for p_{H} value of the medium as well as for nitrogen source. The complex problem of optimal H-ion concentration for the health of higher plants is discussed by Mevius (98), Arrhenius (5) and others. Whether NO_3 or NH_4 may be superior or inferior seems to depend largely on suitable adjustment of the environmental conditions other than nitrogen supply, notably H-ion concentration. The employment of NH_4 salts of strong acids as source of nitrogen is apt to result in H-ion concentration too high for healthy development in many instances. The eventual nutritional effectiveness of NH_4 for any plant seems therefore to be related, in many instances, to the degree of tolerance exhibited by the plant toward such resultant "physiological acidity." Rice appears to have shown generally a high degree of acidity tolerance.

The hypothetical example discussed above may illustrate, as a general and fundamental principle, how important it is to include a representative range of p_{H} values in experimentation on nitrogen sources, and the same general principle requires attention with regard to other influential conditions, not only the concentrations of the other effective non-nitrogenous ions (as Ca^{++} , $\text{HPO}_4^{=}$, etc.) but the total osmotic value of the medium, temperature and temperature fluctuation, light intensity, quality of light and light fluctuation, and so on. Even for an adequately specified kind of plant, in an adequately specified developmental phase, it would be impossible to state definitely that either the NO_3 ion or the NH_4 ion is

always preferable to the other ion, for apparent preference in such a case is clearly conditioned by non-nitrogen features of experimental environment. When field culture is considered the theoretical problem of nitrogen sources becomes vastly more complicated, because of the practical impossibility of even attempting to take all influential environmental features into account. It is consequently not surprising that the very extensive literature of field tests with various nitrogen fertilizers is characterized by even greater discrepancy (at least as far as theory is concerned) than is shown by the literature of physiological cultures with which this paper deals.

As to the other non-nitrogenous ions commonly present in experimental media, the partial concentrations of PO_4 , Ca, Mg, etc., may be expected to influence not only H-ion concentration but also a plant's response to a given concentration of NH_4 or NO_3 when applied along with a specified H-ion concentration. Many different experimental solutions might be made up so as to have the same p_{H} value and the same partial concentration of NH_4 , but they would hardly be expected to be alike in nutrient effectiveness unless their other components had been suitably adjusted. Since the solutions used in different experiments on nitrogen nutrition have been very various with respect to their non-nitrogen constituents (even when their H-ion concentrations have been taken adequately into account) it is easy to suggest possible explanations for apparently discrepant results on this ground alone.

It has been noted that for physiological experimentation (as different from agronomic or other technological studies) soil cultures are unsuitable because of the innumerable unknown variables involved, but sand cultures have been used with relatively satisfactory results by many

students of the problem of nitrogen nutrition, since such cultures bring into account some of the simpler soil features without necessarily complicating the experimentation to a hopeless degree. However, solution cultures naturally furnish the least troublesome procedure for experimentation and for the logical analysis of experimental results. Data derived from sand cultures may be very difficult to compare with corresponding data derived from solution-culture experiments, as is to be seen at various places in the present review. Such comparisons have been made by Shive and W. H. Martin (145), Hoagland and J. C. Martin (56) and Bakke and Erdman (8).

Another important possible source of discrepancy in experimentation on nitrogen sources, as well as on other phases of the problem of salt nutrition, refers to alterations that may occur in nutrient solutions after the plants have been introduced. This suggests not only the comprehensive question of differential absorption and possible excretion by plant roots but also the question of the presence or absence of micro-organisms in the experimental cultures, especially nitrifying and denitrifying bacteria. Trelease and Livingston (155), Allison (3), Allison and Shive (4), Shive and Stahl (146), Pirschle (119, 120, 121, 122) and others have indicated that continuously flowing solutions may be employed to avoid a number of fluctuating variables that are commonly encountered in culture experiments in which solutions are renewed at intervals. Flowing solutions have been employed by several experimenters in the study of nitrogen relations. It does not appear, however, that really satisfactory experimental procedure has thus far been at all widely applied for the prevention or quantitative experimental control of the effects of micro-organisms in culture solutions.

While arrangements are readily feasible by which a solution flowing into a culture jar is surely quite free from micro-organisms, yet it is not so easy to guard against the presence of micro-organisms on the roots of the plants when an experiment is started. Before really satisfactory experimental data on this question of the relative effectiveness of NH_4 and NO_3 can be made available the possibility of both nitrification and denitrification, as well as other changes apt to occur in the medium during a culture period, will need to be guarded against.

When continuous renewal of solutions is not resorted to, the relations between volume of culture jar, size of plants, number of plants per jar, concentrations and salt proportions of solutions, frequency of renewal of solutions and other related features, all surely require to be taken into account quantitatively. Perhaps many of the disagreements and apparent discrepancies of the literature reviewed in this paper may be related to some of these imperfectly understood variables.

Aeration of culture media is another feature of salt-nutrition experimentation that deserves serious attention, not only with reference to oxygen supply but also with reference to CO_2 concentrations and perhaps to concentrations of other volatile substances that may emanate from the roots or arise in the solutions. This feature may be standardized through the use of suitable arrangements for continuous renewal of solutions (3, 4).

Turning to the physical environment of experimental cultures, temperature, light quality, light intensity and fluctuations of light and temperature, are among the unknown or inadequately specified influences to which may be related some of the present confusion concerning nitrogen sources for green plants. Diurnal periodicity of temperature or of light, or both, may well

be of paramount importance. The season of the year at which an experiment is performed may perhaps be indirectly influential in determining what sort of results may be obtained when two different solutions are compared (40).

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